THE CALIFORNIA SPECIES OF ASPIDOTIS

Alan R. Smith[1]
Department of Botany, University of California, Berkeley 94720

Wagner and Gilbert (1957) first described *Aspidotis carlotta-halliae* (Wagner & Gilbert) Lellinger, a rare endemic California fern from Mt. Tamalpais in Marin County. Because *A. carlotta-halliae* is morphologically intermediate between *A. densa* (Brack.) Lellinger [≡ *Cheilanthes siliquosa* Maxon] and *A. californica* (Hook.) Nutt. ex Copel. [≡ *Cheilanthes californica* (Hook.) Mett.] and produces larger spores than either, they hypothesized that it arose by allopolyploidy from a hybrid between the two latter species. Knobloch (1966) reported chromosome numbers of $2n = 30$ II for *A. densa* and *A. californica,* and a count of $2n = 30$ II + 30 I for a presumed backcross of *A. carlotta-halliae* to *A. californica.* The specific status and presumed origin of *A. carlotta-halliae* have not been universally accepted. Howell (1960) expressed doubt about the specific status of *A. carlotta-halliae* because of the variety of intermediates between *A. densa* and *A. californica* at the type locality. Hoover (1966, 1970) considered *A. carlotta-halliae* to be a mere sporadic variant of *A. densa* and reduced it to the status of forma under the latter species.

The diversity of opinions regarding the status of *A. carlotta-halliae* prompted a reinvestigation of its relationships to its postulated parents. All three Californian species were studied morphologically, cytologically, and chromatographically. Hybridization attempts have thus far been inconclusive and are not discussed here. Because of reported substrate preferences of the species, experiments were conducted to determine whether gametophytes differed in growth response on different soils. *Aspidotis densa* grows preferentially on soils derived from serpentine or other ultramafic rocks, not only in California but throughout its range (St. John, 1963; Kruckeberg, 1969). *Aspidotis carlotta-halliae* has been reported only on serpentine (Peñalosa, 1963). On the other hand, *A. californica* is found on soils derived from granitic rocks, or at least not serpentine. Notes from herbarium specimens and field observations substantiate these habitat preferences.

Following Lellinger (1968), I consider these species to belong to *Aspidotis,* a segregate of *Cheilanthes* comprising four North American species,

[1] This study was initiated as a seminar project under the direction of the author at the University of California, Berkeley, in Spring 1972. Participants were James E. Eckenwalder; Fred R. Ganders; Ann M. Hirsch; Dale E. Johnson; Stefan Kirchanski; George E. Pilz; W. Paul Sanders; M. Y. Sheikh; Dan B. Walker; Stephen G. Weller; and Pamela Yorks.

the three already mentioned and *A. meifolia* (D. C. Eaton) Pic.-Ser. from northeastern Mexico. *Aspidotis* is distinguished from *Cheilanthes* by elongate, narrow, generally mucronate-rostrate and distantly toothed frond segments, lack of indument on axes and laminae, striate and shining adaxial surface of laminae, and broad, scarious indusia.

Materials and Methods

Extensive field work was conducted throughout California to locate populations of *Aspidotis*. In addition, approximately 230 herbarium specimens of *A. densa*, 115 of *A. californica*, and 30 of *A. carlotta-halliae* were examined from CAS, DS, and UC. Measurements were made of characters suggested by Wagner and Gilbert (1957), except that basal pinna length was measured instead of blade width. Spore-diameter measurements were recorded for exospore only (perispore excluded).

Chromosome counts were made from sporogenous cells undergoing meiosis, or in a few instances from mitotic cells within sporangia. Fertile fronds were fixed in Carnoy's solution and preparations stained with aceto-carmine. Voucher specimens are in UC; voucher slides are in the author's collection.

Flavonoid chemistry was studied from dried fronds extracted in 0.5 percent HCl in methanol, using 2-dimensional descending paper chromatography with 3:1:1 (v:v:v) tert-butanol:acetic acid:water as the first solvent and 15 percent acetic acid as the second solvent. Collections used in constructing chromatographic profiles are indicated by an asterisk in Table 1. In addition, the following herbarium collections were studied chromatographically: *Howitt 1304* (CAS), *Howell & Leschke s.n.*, 1943 (CAS), and *Hardham 5647* (CAS), all *A. carlotta-halliae; Bacon s.n.*, 1902 (DS), *Saunders s.n.*, 1906 (CAS), *Howell 16925* (CAS), and *Quick 1824* (CAS), all *A. densa.*

Soil and spore samples for use in gametophyte growth studies were collected from the following localities:

1. *A. densa* population. Marin Co., slope above Alpine Lake on Fairfax-Bolinas Rd. Clay-loam soil overlying serpentine.
2. *A. carlotta-halliae* population *(Smith 575H, 2n* = 60 II). Marin Co., Mt. Tamalpais, below Bootjack Camp. Clay-loam soil overlying serpentine.
3. *A. californica* population *(Smith 561, 2n* = 30 II). Monterey Co., Pfeiffer Big Sur State Park, Pine Ridge Trail. Humus and decomposed granite.
4. *A. densa* popuation *(Smith 575E, 2n* = 30 II). Marin Co., Mt. Tamalpais, above Bootjack Camp. Serpentine-derived soil.
5. No *Aspidotis* present. Marin Co., Mt. Tamalpais, above Bootjack Camp. Pulverized serpentine rock.

For gametophyte growth studies, substrates were prepared by tamping a one-inch layer of sterilized soil over a two-inch layer of sterilized vermiculite in culture dishes. Dishes were watered with distilled water.

TABLE 1. CHROMOSOME NUMBERS IN ASPIDOTIS. Collections used in constructing chromatographic profiles are indicated by an asterisk.

Aspidotis californica (Hook.) Nutt. ex Copel. $2n = 30$ II, $2n = 60$ II.
DIPLOIDS: California: Fresno Co., 4.2 km (2.6 mi) N of State Hwy 180 on Elwood Rd, *Smith 636*; Fresno Co., ca 1.5 km (1 mi) S of Maxon Rd and Trimmer Springs Rd, *Smith 637*; Fresno Co., 12.3 km (7.6 mi) W of Big Creek along Trimmer Springs Rd, *Smith 839*; Los Angeles Co., San Gabriel Mts., Eaton Canyon, *Smith 557**; Monterey Co., Pfeiffer Big Sur State Park, Pine Ridge trail, *Smith 561**; San Diego Co., near Pala, *Fischer 4341**; San Diego Co., near Barrett Dam, *Harvey s.n.* [*Knobloch 63–5*] (MSC); Tulare Co., 6.6 km (4.1 mi) E of Springville on State Hwy 190, *Smith 624;* Tulare Co., 9.8 km (6.1 mi) E of Kaweah River along State Hwy 198, *Smith 628*; 11.3 km (7.0 mi) N of State Hwy 216 on J21, *Smith 635*.
TETRAPLOIDS: California: Amador Co., Lancha Plana Road, 1.3 km (0.8 mi) S of intersection with Comanche Parkway, *Smith 648*; Calaveras Co., 0.8 km (0.5 mi) N of Parrots Ferry Bridge, along road to Vallecito, *Smith 602*; El Dorado Co., 10.5 km (6.5 mi) N of Plymouth along State Hwy 49, *Smith 649*; Lake Co., 0.6 km (0.4 mi) W of State Hwy 175 on road to Anderson Springs, *Smith 653*; Marin Co., ca 3 km (2 mi) N of Alpine Lake Dam, *Smith 650*; Mariposa Co., 47.0 km (29.1 mi) NE of Mariposa along State Hwy 140, *Smith 642*; Napa Co., 4.8 km (3.0 mi) ENE of Napa along State Hwy 121, *Smith 658;* Tuolumne Co., Italian Bar, *Smith 599*; Tuolumne Co., 2.7 km (1.7 mi) E of Tuolumne Confidence Rd along Buchanan Rd, *Smith 645*; Tuolumne Co., 5.6 km (3.5 mi) N of Columbia on road to Vallecito, *Smith 646*.

Aspidotis carlotta-halliae (Wagner & Gilbert) Lellinger. $2n = 60$ II, $2n =$ ca 120.
California: Marin Co., Mt. Tamalpais, vicinity of Bootjack Camp, *Smith 575B**, *575D**, *575H, 607, 608, 609, 610, 614;* Marin Co., Bootjack, *Roderick s.n.** [UC Botanical Garden Acc. 62.039]; Monterey Co., Los Padres National Forest, ca 1.5 km (1 mi) downstream from Alder Creek Campground, *Smith 579**, *580, 582, 583, 584, 586, 587, 588, 593, 595, 596, 597*.

Aspidotis densa (Brack.) Lellinger. $2n = 30$ II.
California: Humboldt Co., ca 8 km (5 mi) S of Somes Bar on State Hwy 96, *Smith 572**; Lake Co., 1.8 km (1.1 mi) W of Napa Co. line on Butts Canyon Rd, *Smith 654*; Marin Co., Mt. Tamalpais, along Old Stage Road above Bootjack Camp, *Smith 575C, 575E*; Napa Co., 0.3 km (0.2 mi) N of State Hwy 128 along Berryessa-Knoxville Rd., *Smith 657;* Siskiyou Co., Scott Mt. Rd., ca 6.5 km (4 mi) SE of intersection with road to Callahan, *Smith 570*; Siskiyou Co., ca 8 km (5 mi) E of Somes Bar on State Hwy 96, *Smith 573*; Tuolumne Co., N side of Hetch Hetchy Reservoir, *Yorks 101*. Cultivated plant, *Knobloch 63–9* (MSC).

Aspidotis meifolia (D.C. Eaton in Wats.) Pic.-Ser. $2n = 30$ II.
Mexico: Tamaulipas, W of Victoria, *Knobloch 2251* [UC Botanical Garden Acc. 68.244].

Aspidotis californica × *carlotta-halliae*. $2n = 30$ II + 30 I.
Monterey Co., vicinity of Alder Creek, *Kiefer 1358* (MSC).

Controls were grown on one percent nutrient agar using modified Prague's medium. Spores were suspended in distilled water and about 150 spores delivered to each dish. Number of spores delivered per dish was determined by counting spores in sample aliquots. Culture dishes were placed in a growth chamber, temperature 17°C, fluorescent lights, 350 f.c., photoperiod 16/8 (light/dark).

Results

Morphology (data collected by D. E. Johnson, G. E. Pilz). Morphological studies confirm those of Wagner and Gilbert (1957) in that they show similar directions and magnitudes of differences among the three taxa. *Aspidotis carlotta-halliae* tends to be intermediate between *A. densa* and *A. californica* in all characters examined except petiole length and petiole/blade length ratio. Our data, since they support previous data, are not reproduced here, but are on file with chromosome vouchers in UC.

Relative degree of dissection of indusia in mature fronds appears to be the best single character for separating the taxa, since there is considerable overlap among taxa for other characteristics. Sterile (usually juvenile or early season) fronds of *A. densa* are often more dissected than mature fertile fronds; partially fertile fronds often show more dissection of indusia than do fully fertile fronds, and so may be mistaken for *A. carlotta-halliae*. Nearly all collections identified as forma *carlotta-halliae* by Hoover (1966, 1970) are juvenile, sparingly fertile specimens of *A. densa*. Similarly, juvenile fronds of *A. carlotta-halliae* are more dissected than adult fronds of the same species and may consequently be mistaken for *A. californica*.

Cytology (data collected by A. R. Smith, S. G. Weller). Chromosome counts for *Aspidotis* are listed in Table 1; three previous counts by Knobloch (1966) are indicated by location of the voucher (MSC). These counts show that *A. carlotta-halliae* is indeed polyploid ($2n = 60$ II), as predicted by Wagner and Gilbert (1957). All counts of *A. densa* are diploid ($2n = 30$ II).

Unexpectedly, *A. californica* proved to consist of both diploid and tetraploid cytotypes (Table 1). Diploid plants occur in the Coast Ranges from Monterey Co. to San Diego Co. and also in the foothills of the Sierra Nevada from Kern Co. to Tuolumne Co.; tetraploids occupy the northern half of the distribution of *A. californica*, occurring in the North Coast Ranges from Marin Co. to Mendocino Co. and in the Sierra Nevada foothills from Mariposa Co. to Butte Co. Figure 1 illustrates the distribution of the two cytotypes as judged from both chromosome counts and spore measurements. There is a narrow area of apparent sympatry—apparent because the two cytotypes have not yet been found growing together—in Tuolumne and Mariposa counties. In the Sierra Nevada, the two cytotypes are very similar morphologically, but tetraploids are generally more robust and thicker-textured than diploids, and spore diameter in the tetraploids is larger. However, small-spored diploids from southern California attain or even surpass the Sierra Nevada tetraploids in robustness.

Spore morphology (data collected by M. Y. Sheikh). Because relative spore size is often useful in predicting ploid among closely related species, we measured spore diameter in *Aspidotis* (Table 2). Wagner and Gilbert (1957) found that spores of *A. carlotta-halliae* were larger than spores of either *A. densa* or *A. californica*. Our measurements confirm

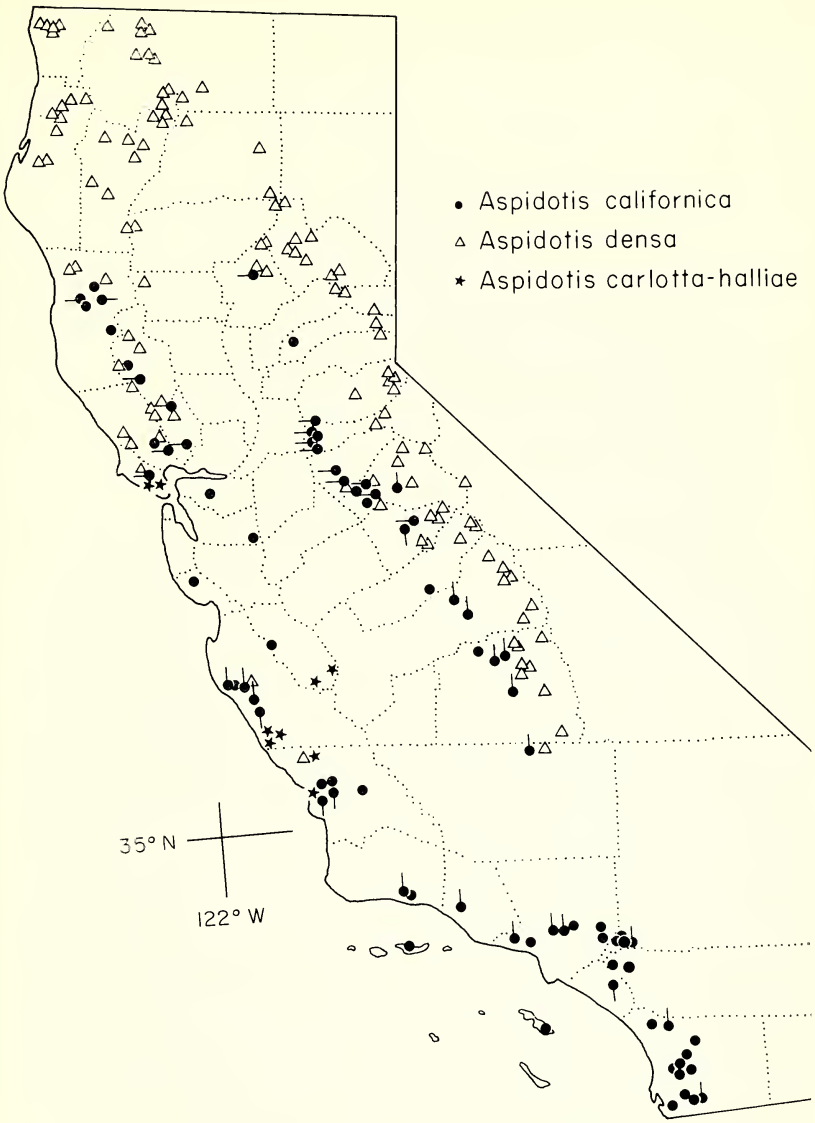

FIG. 1. Distribution of *Aspidotis* in California. Symbols with vertical rays indicate collections known to be diploid from chromosome counts or judged to be diploid from spore measurements. Symbols with horizontal rays indicate collections known to be tetraploid from chromosome counts or judged to be tetraploid from spore measurements.

this only when suspected diploids of *A. californica* are considered, but known tetraploids of *A. californica* (e.g., *Smith 602;* spores 46–59 μm, mean 52 μm) have spores similar in size to spores of *A. carlotta-halliae*

TABLE 2. SPORE DIAMETERS IN ASPIDOTIS SPP. Mature spore and meiotic stages are rarely present in single plants at the same time; both chromosome number and spore size are available for only one plant (cited in text). Ploidal levels (number of populations sampled given in parentheses) are summarized from data in Table 1. N = number of specimens sampled. Ten spores were measured for each specimen.

Taxon	N	Range of sample means, μm	Absolute range, μm
A. densa, 2*x* (8) (California)	10	39–45	35–49
A. carlotta-halliae, 4*x* (2) (California)	10	48–58	42–64
A. californica, 2*x* (4) (Coast Ranges, Monterey Co. to San Diego Co.)	10	39–44	30–48
A. californica, 2*x* (6) (Sierra Nevada, Tuolumne Co. to Kern Co.)	6	40–44	37–48
A. californica, 4*x* (10) (Sierra Nevada, Butte Co. to Mariposa Co.; N Coast Ranges)	10	47–51	42–60

(Table 2). Sporangial size, length and width of spore laesurae, and perispore thickness all are correlated to some extent with spore size, being larger or thicker in *A. carlotta-halliae* and tetraploid *A. californica* than in diploid *A. californica* or *A. densa*. Additionally, there are subtle differences in spore ornamentation among species of *Aspidotis*. The perispore in *A. californica* and *A. carlotta-halliae* is somewhat more fimbriate than in *A. densa* but less fimbriate than in *A. meifolia*.

Flavonoid chemistry (data collected by J. E. Eckenwalder). Considerable chromatographic variation occurs among populations of the same species. Nevertheless, except for some anomalous specimens of *A. californica* from southern California, chromatograms of both *A. densa* and *A. californica* possess characteristic spots, shown in the composite chromatogram (fig. 2). Most importantly, chromatograms of *A. carlotta-halliae* showed characteristic spots of both *A. densa* and *A. californica*. Spots 7, 9, and 27 were present in nearly all collections of *Aspidotis;* spots 24, 25, and 35 were present in *A. densa* and *A. carlotta-halliae,* but absent in *A. californica;* and spot 12 was present in *A. californica* and *A. carlotta-halliae,* but absent in *A. densa*. Two additional spots, 13 and 32, were often absent in *A. densa,* but present in *A. californica* and *A. carlotta-halliae*. Tetraploid material of *A. californica* has not yet been tested chromatographically.

Gametophytes (data collected by D. Walker, W. P. Sanders, and F. Ganders). Gametophyte growth on different natural soils was determined after 18 weeks. Gametophytes were counted, and spore germination percentages for each species on each soil are given in Table 3 (one standard deviation given for number of spores plated and percent germination). All species showed greater than 75 percent germination on

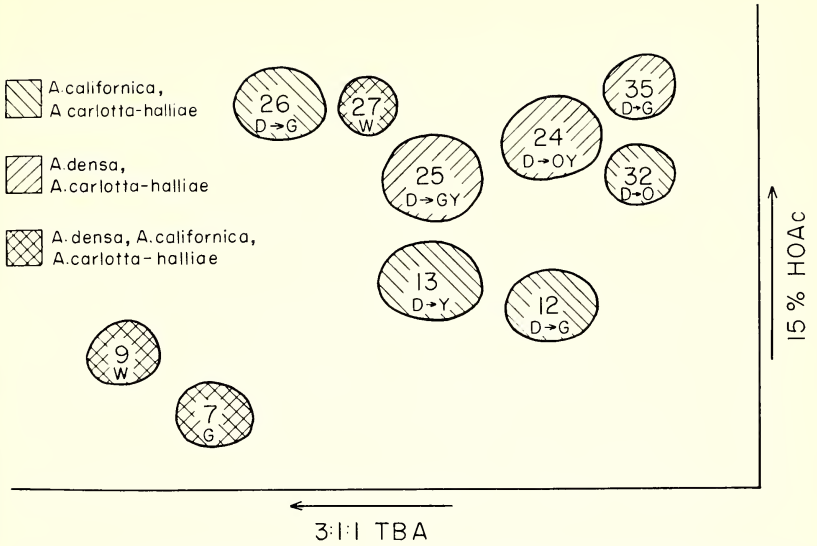

FIG. 2. Composite chromatogram of *Aspidotis* spp. in California. Color reactions under UV light are given beneath spot number: B = Blue; G = Green; O = Orange; W = White; Y = Yellow; D = Absorbing. Arrows point to color change when viewed under UV + NH_3. Spots 13 and 32 were infrequently present on chromatograms of *A. densa*.

agar, indicating high spore viability. With few exceptions, *A. densa* spores showed the highest germination percentages on all soils, *A. californica* was next, and *A. carlotta-halliae* the lowest. In general, spore germination percentages in all species were correlated with particle size of the soil, germination and growth being favored by smaller-particled substrates such as the clay-loam soils. This is probably related to the water-holding capacity of the soils, which is inversely proportional to particle size.

The data show no correlation between spore germination and the soil on which sporophytes are found. The virtual absence of germination and growth on pure serpentine rock is probably due to its poor water-holding capacity but could be due to inhibition by some chemical factor. Gametophyte requirements do not appear to be responsible for the edaphic preferences exhibited by sporophytes in nature. Other factors, such as moisture, competition, and sporophytic requirements must restrict these ferns to their respective habitats.

Number of spores per sporangium is consistently 64 for all four species of *Aspidotis*, suggesting that they are sexual and that apogamy is not a typical feature of their life cycle, as it is in many cheilanthoid ferns. Gametophytes of all species are initially female and later become hermaphroditic. Development of archegonia before antheridia is supposedly uncommon in fern gametophytes, but is the normal sequence in

TABLE 3. SPORE GERMINATION OF ASPIDOTIS SPP. ON VARIOUS SUBSTRATES. Numbers preceding species names refer to populations from which spores and substrate were obtained (see Materials and Methods). Percent germination is included parenthetically after number of spores germinated.

Substrate source	1. *A. densa* 150 ± 14.8 spores plated	3. *A. californica* 142 ± 8.5 plated	2. *A. carlotta-halliae* 144 ± 8.4 plated
Nutrient agar	122 (81.4 ± 7.3)	164[a] (115.2 ± 6.2)	109 (75.8 ± 4.3)
1. *A. densa;* clay-loam	138 (92.0 ± 8.1)	109 (76.7 ± 4.2)	94 (65.3 ± 3.7)
2. *A. carlotta-halliae;* clay-loam	128 (85.4 ± 7.6)	124 (87.2 ± 4.7)	89 (61.8 ± 3.4)
4. *A. densa;* serpentine-derived soil	82 (54.6 ± 4.8)	60 (42.2 ± 2.3)	77 (53.5 ± 3.0)
3. *A. californica;* humus decomposed granite	73 (48.6 ± 4.3)	50 (35.2 ± 2.0)	38 (26.4 ± 1.5)
5. No *Aspidotis*; crushed serpentine rock	1 (0. ± 0.1)	0 (0.)	0 (0.)

[a] Higher than expected germination probably due to clumping of spores at time of plating, as evidenced by a few clumps of gametophytes. Clumping was ordinarily not a problem, with gametophytes distributed more or less randomly.

Aspidotis, many Blechnaceae (Klekowski, 1969b), and several other ferns. This has been interpreted as an adaptation for outcrossing (Klekowski, 1969a).

DISCUSSION AND CONCLUSION

Aspidotis carlotta-halliae is morphologically intermediate between *A. densa* and *A. californica,* shows additive flavonoid chemistry, and is a fertile, sexual tetraploid. It shows slightly lower spore germination percentages than its diploid relatives. Tetraploids derived from diploid hybrids often show reduced fertility (Stebbins, 1950). Gametophytes of all three Californian species are capable of growth on serpentine or non-serpentine soils in laboratory cultures. These gametophytes develop sex organs in a sequence that is thought to promote intergametophytic mating.

The alleged backcross reported by Knobloch (1966) remains enigmatic. The voucher *(Kiefer 1358,* Knobloch Acc. 64–20, MSU!) is a typical specimen of *A. carlotta-halliae.* I have reexamined voucher slides prepared by Knobloch and also slides made by Wagner from plants of the same collection *(Kiefer 1358,* MICH!) and concur that the chromosome complement of cells at meiosis is ca 30 II + 30 I. I have also revisited the locality in question and obtained chromosome counts from thirteen plants throughout the population. All plants showed unequivocally either $2n = 60$ II, with normal pairing behavior at meiosis, or $2n = 120$ in somatic cells (Table 1). Neither *A. californica* nor *A. densa* could be found in the immediate area, although they certainly could occur there (or might have occurred in the past). One explana-

tion for these seemingly disparate facts is that the chromosome voucher at MSU may not be the plant actually counted—that within the original gathering by Kiefer there were both *A. carlotta-halliae* and the backcross to *A. californica.* In support of this hypothesis is the fact that another collection of *Kiefer 1358* at MSU (!) seems more likely to be a backcross. Alternatively, the backcross could be morphologically so like *A. carlotta-halliae* that the two would be indistinguishable without cytological or palynological data.

The distribution of *A. carlotta-halliae* is rather limited, with a much smaller range than either of its presumed parent species. Wagner and Gilbert (1957) recorded it from three counties in the Coast Ranges: Marin, San Benito, and San Luis Obispo. It is now known from several stations in Monterey Co. and from additional localities in all of the first three counties (fig. 1). At the type locality, Bootjack Camp, Marin Co., there is a large population of *A. carlotta-halliae,* but, contrary to Howell (1960), neither *A. densa* nor *A. californica* could be found in this population. *Aspidotis densa* is abundant nearby in chaparral and on serpentine above Bootjack Camp and actually grows with *A. carlotta-halliae* along a narrow interface between chaparral and woodland. This is the only area where I know of two species of *Aspidotis* growing together. Hybrids have not yet been found along this interface. *Aspidotis californica* is apparently much rarer in Marin Co., where it was found growing at the bases of decomposing granitic boulders. It is probable that in the Coast Ranges edaphic preferences prevent all but rare contact between *A. densa* (on serpentine) and *A. californica* (on non-serpentine). In the Sierra Nevada, elevational differences separate the two species, with *A. densa* occurring at higher elevations (on or off of serpentine). *Aspidotis californica* has not yet been found growing with either *A. densa* or *A. carlotta-halliae.* The two cytotypes of *A. californica* occupy similar habitats, but tetraploids have seemingly adapted to a greater variety of situations (e.g., wet, rocky gullies and heavily shaded woodlands, as well as rocky outcrops) than have diploids.

Present distributions of the Californian species (fig. 1) show two areas where all three species occur and where the allotetraploid *A. carlotta-halliae* might have evolved: northern San Luis Obispo Co.-southern Monterey Co., and Marin Co. Since the diploid cytotype of *A. californica* is thus far unknown from Marin Co., one suspects that the origin of *A. carlotta-halliae* may have been in the first-mentioned area. Less certain is the origin of tetraploid *A. californica.* The two cytotypes of *A. californica* are close enough morphologically to suggest that autopolyploidy has occurred. There are slight differences in size and texture of fronds, especially in the Sierra Nevada, but there seems to be little basis for taxonomic recognition of the cytotypes other than perhaps as geographical varieties. No one, heretofore, has recognized discontinuity within *A. californica.* Additional chemical study seems the best avenue for shedding light on the origin of the tetraploid cytotype.

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TAXONOMY OF PSATHYROTES (COMPOSITAE: SENECIONEAE)

John L. Strother and George Pilz
Department of Botany, University of California, Berkeley 94720

Psathyrotes comprises five species of humble herbs, two in the Chihuahuan Desert and three in the Sonoran Desert and southwestern Great Basin. They typically grow in dry, sandy washes, among sand dunes, or on gravelly benches and alluvial fans. Economically these plants are are of no known consequence; aesthetically they are not particularly appealing. They have received little attention from botanists other than compilers of regional floras and, therefore, have been relatively poorly known. Heretofore, morphological circumscriptions of at least two species and geographic ranges of three have been confusedly or inaccurately delineated in regional and local floras. We hope that our observations will serve to abrogate the confusion and to redress the inaccuracies.

A brief chronology of the taxonomic history of the genus follows:

1848. Nuttall described the first plant to be assigned to the genus, *Bulbostylis annua,* placing it in a monotypic section, *Psathyrotus* [sic]. (*Bulbostylis* DC. is now generally considered to be a synonym of *Brickellia* Ell., a member of Eupatorieae.) Later in the same year, Torrey named a new species, *Tetradymia ramosissima,* placing it in a new, monotypic subg. *Polydemia*. (*Tetradymia* is a member of Senecioneae.)